

PLANT PHYSIOLOGY

LINCOLN TAIZ UNIVERSITY OF CALIFORNIA, SANTA CRUZ

EDUARDO ZEIGER UNIVERSITY OF CALIFORNIA, LOS ANGELES



The Benjamin/Cummings Publishing Company, Inc. Redwood City, California • Menlo Park, California • Reading, Massachusetts New York • Don Mills, Ontario • Wokingham, U.K. • Amsterdam • Bonn Sydney • Singapore • Tokyo • Madrid • San Juan

CONTENTS

PREFACE v

ABOUT THE AUTHORS vii CONTRIBUTORS vii REVIEWERS ix

PHOTOGRAPH AND ILLUSTRATION CREDITS xi



OVERVIEW OF ESSENTIAL CONCEPTS 1

CHAPTER 1 Plant and Cell Architecture 3

Plant Life: Unifying Principles 3 The Plant Kingdom 4 The Plant: An Overview of Structure 6 New Cells Are Produced by Dividing Tissues Called Meristems 7 Plants Are Composed of Three Major Tissues 8 The Plant Cell 9 Biological Membranes Are Phospholipid Bilayers Containing Proteins 9 The Nucleus Contains the Genetic Material of the Cell 11 The Genome Size of Higher Plants Is Quite Variable 11 Ribosomes Are Formed in the Nucleolus and Are the Sites of Protein Synthesis 12 The Endoplasmic Reticulum Is the Major Network of Internal Membranes in the Cell 15 Secretory Proteins and Polysaccharides Are Processed and Sorted in the Golgi 16 The Vacuole Occupies Most of the Volume of the Mature Plant Cell 16 Mitochondria and Chloroplasts Are Sites of Energy Conversion 17 Most Mitochondrial and Chloroplast Proteins Are Imported from the Cytosol During Organelle Assembly 19 Microbodies Play Specialized Metabolic Roles in Leaves and Seeds 19

The Cytoskeleton 20

Microtubules and Microfilaments Can Assemble and Disassemble 20 Microtubules Function in Mitosis and Cytokinesis 20

The Preprophase Band of Microtubules Determines the Plane of Cytokinesis 22

Microfilaments Are Involved in Cytoplasmic Streaming and Tip Growth 22 The Plant Cell Wall 22

The Primary Cell Wall Is Composed of Cellulose Microfibrils and Matrix Material 22

Secondary Walls Differ in Their Composition and Mechanical Properties from Primary Walls 23

The Wall Matrix Is Secreted Via Golgi Vesicles While Cellulose Is Synthesized on the Plasma Membrane 23

Plant Cells Are Interconnected by Membrane-Lined Channels Called Plasmodesmata 25

Summary 26

General Reading 27

Chapter References 27

CHAPTER 2 Energy, Enzymes, and Gene Expression 28

Energy Flow Through Living Systems 28 Energy and Work 29 The First Law: The Total Energy Is Always Conserved 29 The Change in the Internal Energy of a System Represents the Maximum Work It Can Do 30 Each Type of Energy Is Characterized by a Size Factor and a Potential Factor 30 The Direction of Spontaneous Processes - 31 The Second Law: The Total Entropy Always Increases 31 A Process Is Spontaneous if ΔS for the System and Its Surroundings Is Positive 32 Free Energy and Chemical Potential 32 ΔG Is Negative for a Spontaneous Process at Constant Temperature and Pressure 32 The Standard Free Energy, ΔG° , Is the Free Energy Change When the Concentration of Reactants and Products Is 1 M 33 The Value of ΔG is a Function of the Displacement of the Reaction from Equilibrium 33 The Enthalpy Change Measures the Energy Transferred as Heat 34 Redox Reactions 34 The Free Energy Change of an Oxidation-Reduction Reaction Is Expressed as the Standard Redox Potential in Electrochemical Units 35 The Electrochemical Potential 35 Transport of an Uncharged Solute Against Its Concentration Gradient Decreases the Entropy of the System 35 The Membrane Potential Is the Work That Must Be Done to Move an Ion from One Side of the Membrane to the Other 36 The Electrochemical Potential Difference, $\Delta \mu$, Includes Both Concentration and Electrical Potentials 36 The Water Potential Is the Chemical Potential of Water Expressed in Units of Pressure 37 Enzymes: The Agents of Life 39 Proteins Are Chains of Amino Acids Joined by Peptide Bonds 39 Protein Structure Is Hierarchical 41

Enzymes Are Highly Specific Protein Catalysts 43

Enzymes Lower the Free Energy Barrier Between Substrates and Products 43 Catalysis Occurs at the Active Site 44 A Simple Kinetic Equation Describes an Enzyme-Catalyzed Reaction 44 Enzymes Are Subject to Various Kinds of Inhibition 46 pH and Temperature Affect the Rate of Enzyme-Catalyzed Reactions 47 Cooperative Systems Increase the Sensitivity to Substrates and Are Usually Allosteric 47 The Kinetics of Some Membrane Transport Processes Can Also Be Described by the Michaelis-Menten Equation 48 Enzyme Activity Is Often Regulated 48 Gene Expression and Protein Turnover 50 DNA-Binding Proteins Regulate Transcription in Prokaryotes 51 Gene Expression in Eukaryotes Is Regulated at Many Levels 52 Transcription in Eukaryotes Is Also Regulated by DNA-Binding Proteins 54 Protein Turnover Is an Important Factor Affecting Enzyme Levels in Cells - 55 Summary 55 General Reading 56 Chapter References 57



TRANSPORT AND TRANSLOCATION OF WATER AND SOLUTES 59

CHAPTER 3 Water and Plant Cells 61

The Structure and Properties of Water 62

The Polarity of Water Molecules Gives Rise to Extensive Intermolecular Attractions Called Hydrogen Bonds 62

The Polarity of Water Makes It an Excellent Solvent 62

The Ability of Water to Form Hydrogen Bonds Gives Rise to Its Thermal, Cohesive, and Adhesive Properties 63

Water Has a High Tensile Strength 64

Transport Processes 65

Diffusion Is the Movement of Molecules Along a Concentration Gradient by Random Thermal Agitation 65

The Rate of Diffusion Is Rapid over Short Distances but Extremely Slow over Long Distances 65

Long-Distance Water Transport in the Plant Occurs by Bulk Flow 66

Osmosis, the Movement of Water Through a Selectively Permeable Membrane, Involves Both Bulk Flow and Diffusion 67

The Chemical Potential of Water or "Water Potential" Represents the Free Energy Status of Water 67

The Major Factors Contributing to Water Potential Are Represented by the Equation $\Psi = P - \pi$ 68

Water Enters the Cell Along a Water Potential Gradient Until the Water Potential Inside Equals the Water Potential Outside 70

Because of the Rigid Cell Wall, Small Changes in Cell Volume Cause Large Changes in the Turgor Pressure 70

Water Can Also Leave the Cell in Response to a Water Potential Gradient 70 The "Matric Potential" Is the Overall Reduction in Water Potential Caused by

Insoluble Materials Such as Soil Colloids or Cell Walls 76

The Water Potential Concept Is Useful for Evaluating the Water Status of a Plant 76 The Rate of Water Transport Depends on the Magnitude of the Driving Force and the Hydraulic Conductivity of the Transport Pathway 78

Summary 79

ESSAY How Water Potential Is Measured 72 General Reading 79 Chapter References 80

CHAPTER 4 Water Balance of the Plant 81

Water in the Soil 81

 Soil Water Potential Is a Function of the Osmotic Pressure of the Soil Water and the Negative Hydrostatic Pressure Caused by Adhesion and Surface Tension 82

Water Moves Through the Soil by Bulk Flow at a Rate Governed by the Pressure Gradient and the Soil Hydraulic Conductivity 82

Water Absorption by the Root 84

Water Crosses the Root Radially Via the Apoplast, Transmembrane, and Symplast Pathways Until It Reaches the Endodermis 84

When Transpiration Is Prevented, Solute Accumulation in the Xylem Can Generate Positive Hydrostatic Pressure or "Root Pressure" 85

Water Is Conducted Through Hollow Tracheids and Vessels of the Xylem 86 The Pressure Gradient Required to Move Water Through the Xylem Is Much

Less Than That Required to Transport Water Through Living Cells 86 A Pressure Gradient of About 3 MPa Is Needed to Lift Water to the Top of a 100-Meter Tree 88

The Conducting Cells of the Xylem Are Adapted for the Transport of Water Under Tension 88

The Source of Tension in the Xylem Is the Negative Pressure That Develops in the Leaf Cell Walls When Water Evaporates 89

Water Vapor Moves from the Leaf to the Atmosphere by Diffusion Through Stomata 90

The Driving Force for Water Loss from the Leaf to the Atmosphere Is the Absolute Concentration Gradient of Water Vapor 92

Transpiration Is Also Regulated by the Leaf Stomatal Conductance and the Boundary Layer Resistance 93

Stomatal Control Serves to Maximize Photosynthesis While Minimizing Transpiration 94

The Radial Orientation of Cellulose Microfibrils in Guard Cell Walls Is Required for Pore Opening 94

Stomatal Opening Is Caused by an Increase in the Turgor Pressure of the Guard Cells 96

The Transpiration Ratio Is a Measure of the Effectiveness of the Stomata in Maximizing Photosynthesis While Minimizing Water Loss 97

Overview: The Soil-Plant-Atmosphere Continuum 97 Summary 98

Summary VY Irrigation

ESSAY

Irrigation 83 General Reading 99 Chapter References 99

CHAPTER 5 Mineral Nutrition 100

The Plant Root System and Its Interaction with the Soil 100 Below the Soil Surface, Plant Roots Are Continuously Growing and Decaying in

Response to Changes in the Soil Environment 101

Some Minerals Enter the Roots at the Apical Region; Others Can Be Taken Up Along the Entire Root Surface 102 Soil and Minerals 104 Negative Charges on the Surface of Soil Particles Affect the Adsorption of Mineral Cations and Anions 104 Nutrient Availability, Soil Microbes, and Root Growth Are Strongly Dependent on Soil pH 105 Mycorrhizal Fungi and Their Association with Plant Roots 106 Mycorrhizal Fungi Grow Inside the Plant Roots and in the Surrounding Soil, Often Facilitating Mineral Uptake by the Plant 106 Leakage and Death of the Fungal Hyphae Are Probably Involved in the Transfer of Nutrients from the Mycorrhizal Fungi to the Plant 107 Essential Elements 107 An Essential Element Is Needed for Completion of the Life Cycle of the Plant, Causes a Specific Deficiency When Unavailable, and Has a Defined Role in Plant Metabolism 108 Techniques for Growing Plants in Nutritional Studies 109 Plant Physiologists Have Formulated Nutrient Solutions That Can Sustain Optimal Plant Growth 110 Roles of Essential Elements and Nutrient Disorders 111 Deficiency of an Essential Element Causes Typical Symptoms Resulting from the Disruption of Metabolic Processes in the Plant 112 Soil and Plant Tissue Analysis as Indicators of Plant Nutritional Status 116 Chemical Fertilizers, Organic Farming, and Foliar Nutrition 116 Crop Yields Can Be Improved by Addition of Chemical or Organic Fertilizers 117 Application of Mineral Nutrients to the Leaves Can Enhance Absorption 117 Salt Stress and Halophytes 117 Summary 118 Looking at Roots Face to Face 103 ESSAY General Reading 118 Chapter References 119

CHAPTER 6 Solute Transport 120

Passive and Active Transport 120

Transport of Solutes Across A Membrane Barrier 122

- A Diffusion Potential Develops When Oppositely Charged Ions Are Transported Across a Cell Membrane at Different Rates 123
- The Nernst Equation Describes the Relationship Between the Voltage Difference Across a Membrane and the Distribution of a Given Ion Under Equilibrium Conditions 123
- The Goldman Equation Describes the Relationship Between the Diffusion Potential and Prevailing Ion Gradients Across a Membrane 124
- Transport Across Biological Membranes 125
 - Two Main Types of Membrane Proteins Enhance the Movements of Substances Across Membranes 125
 - Measurements of Concentrations and Membrane Potentials Can Distinguish Between Active and Passive Transport 126
 - Electrogenic Proton Transport Is a Major Determinant of the Membrane Potential 127
 - Electrogenic Calcium Transport by an ATPase Regulates Intracellular Calcium Concentrations 130

Cotransport Processes Use the Energy Stored in the Proton Motive Force 130 Solute Accumulation in the Vacuole Is Driven by the Tonoplast H⁺-ATPase 132

	Proton Pumping in Guard Cells Generates Ion Gradients That Regulate Guard
	Lon Concentrations in Cuard Colls Increase During Segmental Opening and
	Decrease During Stomatal Opening and
	Decrease During Stomatal Closing 134
	Specific Mechanisms in Guard Cells Mediate the Stomatal Response to
	Light 134
	Light Activates a Proton Pump at the Guard Cell Plasma Membrane 136
	Kinetic Analysis of Transport Processes Can Reveal How Cells Regulate Their
	Intracellular Solute Concentrations 138
	Transcellular Transport 140
	The Apoplast and the Symplast Are the Major Pathways for Solute Movement
	Within the Plant 141
	Ions Moving Through the Root Cross Both Symplastic and Apoplastic
	Spaces 141
	Uptake of Ions into the Xylem Could Involve One or Two Active Pump
	Sites 142
	Summary 143
ESSAY	Chemiosmosis in Action 129
ESSAY	Patch Clamp Studies in Plant Cells 137
	General Reading 143
	Chapter References 144

CHAPTER 7 Phloem Translocation 145

Pathways of Translocation 145 Experiments with Radioactive Labels Show That Sugar Is Translocated in Phloem Sieve Elements 146 Mature Sieve Elements Are Living Cells That Are Highly Specialized for Translocation 148 The Most Characteristic Feature of the Sieve Elements Is the Presence of the Sieve Areas 148 P-Protein and Callose Deposition Seal Off Damaged Sieve Elements 151 The Highly Specialized Sieve Elements Are Functionally Supported by the Companion Cells 152 Patterns of Translocation 153 Source-to-Sink Pathways Follow Anatomical and Developmental Rules 153 Materials Translocated in Phloem 153 Phloem Sap Can Be Collected and Analyzed 154 Sugars Are Translocated in Nonreducing Form 156 Transport Patterns of Nitrogenous Compounds in the Phloem and Xylem Are Interrelated 156 Rates of Movement 158 Velocities of Phloem Transport Average One Meter per Hour 158 Phloem Loading 158 Phloem Loading of Sugar Requires Metabolic Energy 158 The Pathway from the Mesophyll Cells to the Sieve Elements Is at Least Partly Apoplastic 159 Phloem Loading Is Specific and Selective 160 Not All Substances Transported in the Phloem Are Actively Loaded into the Sieve Elements 161 Sucrose Loading Is Driven by a Proton Gradient Generated at the Expense of ATP 161 Phloem Unloading and Sink-to-Source Transition 162 Phloem Unloading and Transport into Receiver Cells Can Be Symplastic or Apoplastic 162

Transport into Sink Tissues Depends On Metabolic Activity 163 The Active Transport Step During Apoplastic Unloading Depends On the Species and Organ 163 The Transition from Sink to Source Is a Gradual Developmental Process in Leaves 164 The Mechanism of Phloem Translocation 164 Active and Passive Mechanisms Have Been Proposed to Account For Phloem Translocation 165 According to the Pressure-Flow Hypothesis, Translocation in the Phloem Is Driven by a Pressure Gradient from Source to Sink 165 Predictions of the Pressure-Flow Model 166 The Sieve-Plate Pores Are Essentially Open Channels Connecting One Sieve-Tube Member to Another 167 Bidirectional Transport in a Single Sieve Element Has Not Been Demonstrated 167 The Rate of Translocation Is Relatively Insensitive to the Energy Supply of the Path Tissues 167 Pressure Gradients in the Sieve Elements Are Sufficient to Drive a Mass Flow of Solution 168 The Mechanism of Phloem Transport in Gymnosperms May Be Different from That in Angiosperms 168 Assimilate Allocation and Partitioning 169 Allocation Includes the Storage, Utilization, and Transport of Fixed Carbon in the Plant 169 Once Synthesized, Transport Sugars Are Partitioned Among the Various Sink Tissues 169 Allocation in Source Leaves Is Regulated by Key Enzymes 170 Sink Tissues Compete for Available Translocated Assimilate 171 Sink Strength Is a Function of Sink Size and Sink Activity 171 Changes in the Source-to-Sink Ratio Bring About Long-Term Alterations in Source Metabolism 172 Turgor Pressure May Directly Regulate the Responses of Sources and Sinks 172 Plant Hormones May Act as Long-Distance Messengers Between Sources and Sinks 172 Summary 173 Monitoring the Traffic on the Sugar Freeway 148 General Reading 173 Chapter References 174

UNIT II

ESSAY



BIOCHEMISTRY AND METABOLISM 177

CHAPTER 8 Photosynthesis: The Light Reactions 179

Photosynthesis in Higher Plants 179

General Concepts and Historical Background 180

Light Has Characteristics of Both a Particle and a Wave 180

When Molecules Absorb or Emit Light They Change Their Electronic State 184

The Quantum Yield Gives Information About the Fate of the Excited State 185 Photosynthetic Pigments Absorb the Light That Powers Photosynthesis 187

Photosynthesis Takes Place in Complexes Containing Light-Gathering Antennas and Photochemical Reaction Centers 188 The Chemical Reaction of Photosynthesis Is Driven by Light 189 Photosynthesis Is a Light-Driven Redox Process 189 Oxygen-Evolving Organisms Have Two Photosystems That Operate in Series 190 Structure of the Photosynthetic Apparatus 191 The Chloroplast Is the Site of Photosynthesis 192 Thylakoids Contain Integral Membrane Proteins 192 The Structures of Two Bacterial Reaction Centers Have Been Determined 195 Photosystems I and II Are Spatially Separated in the Thylakoid Membrane 195 Organization of Light-Absorbing Antenna Systems 197 The Antenna Funnels Energy to the Reaction Center 198 Carotenoids Serve as Both Accessory Pigments and Photoprotective Agents 198 Thylakoid Stacking Is Involved in Energy Partitioning Between the Photosystems 199 Phycobilisomes and Chlorosomes Are Pigment-Protein Complexes That Are Peripherally Associated with the Photosynthetic Membrane 199 Mechanisms of Electron and Proton Transport 201 Electron and Proton Transport Is Carried Out by Four Thylakoid Protein Complexes 204 Energy Storage Takes Place When an Excited Chlorophyll Reduces an Electron Acceptor Molecule 204 The Reaction Center Chlorophylls of Photosystems I and II Have Maximal Absorbances at 700 and 680 nm, Respectively 205 The Photosystem II Reaction Center Complex Oxidizes Water and Reduces Plastoquinone 206 Water Is Oxidized to Oxygen by Photosystem II 206 The Acceptor Region of Photosystem II Contains Pheophytin and Two Quinones as Electron Carriers 208 Electron Flow Through the Cytochrome b_{6} -f Complex Results in Proton Accumulation in the Thylakoid Lumen 209 Plastoquinone and Plastocyanin Are Candidates for Diffusible Intermediates 210 The Photosystem I Reaction Center Reduces NADP⁺ 211 Some Herbicides Kill Plants by Blocking Photosynthetic Electron Flow 211 A Chemiosmotic Mechanism Converts the Energy Stored in Chemical and Membrane Potentials to ATP 212 The Entire Chloroplast Genome Has Been Sequenced 215 Chloroplast Genes Exhibit Non-Mendelian Patterns of Inheritance 215 Many Chloroplast Proteins Are Imported from the Cytoplasm 215 Summary 216 ESSAY **Principles of Spectrophotometry** 181 ESSAY **Midpoint Potentials and Redox Reactions** 202 General Reading 216 Chapter References 217

CHAPTER 9 Photosynthesis: Carbon Metabolism 219

The C3 Photosynthetic Carbon Reduction Cycle 219

The C3 PCR Cycle Includes Carboxylation, Reduction, and Regeneration Steps 220

The PCR Cycle Was Elucidated Using Radioactive Carbon Compounds 226 During Its Operation, the C3 PCR Cycle Regenerates Its Own Biochemical Components 226

The C3 PCR (Cycle Is Regulated by Light-Dependent Enzyme Activation	, by
Ionic Chan	ges in the Stroma, and by Transport Processes in the Chlor	oplast
Envelope	227	

The C2 Photorespiratory Carbon Oxidation (PCO) Cycle 229

Photosynthetic CO₂ Fixation and Photorespiratory Oxygenation of Ribulose 1,5-Bisphosphate Are Competing Reactions at the Same Active Site of Rubisco 229

Competition Between the Carboxylation and Oxygenation Reactions in Vivo Decreases the Thermodynamic Efficiency of Photosynthesis 232

The Relationship Between Carboxylation and Oxygenation in the Intact Leaf Depends On the Kinetic Properties of Rubisco, Prevailing Temperatures, and the Concentrations of CO₂ and O₂ 232

The Biological Function of Photorespiration Remains an Intriguing Question in Biology 233

CO₂ Concentrating Mechanisms I: Algal and Cyanobacterial CO₂/HCO₃ Pumps 233

CO₂ Concentrating Mechanisms II: The C4 Photosynthetic Carbon Assimilation (PCA) Cycle 234

The C4 PCA Cycle Increases the Concentration of CO₂ in the Bundle Sheath Cells 234

Malate and Aspartate Are the First Stable Products of Carboxylation by the C4 PCA Cycle 239

The Energy Cost of Concentrating CO₂ in the Bundle Sheath Cells Lowers the Efficiency of Photosynthesis 239

Light Regulates the Activity of Key Enzymes of the C4 PCA Cycle 240

In Hot, Dry Climates, the Operation of the C4 PCA Cycle Reduces Photorespiration and Water Loss 241

CO₂ Concentrating Mechanisms III: Crassulacean Acid Metabolism (CAM) 241 CAM Plants Open Their Stomata at Night and Keep Them Closed During the Day 241

CAM Metabolism Is Regulated by Different Forms of the Enzyme Phosphoenolpyruvate Carboxylase 241

Synthesis of Sucrose and Starch 243

Starch Is Synthesized and Stored in the Chloroplast While Sucrose Synthesis Takes Place in the Cytosol 243

The Syntheses of Sucrose and Starch Are Competing Reactions Regulated by Key Metabolites 247

Chapter Summary 248

ESSAY Carbon Dioxide: Some Important Physicochemical Properties 221 General Reading 248 Chapter References 248

CHAPTER 10 Photosynthesis: Physiological and Ecological Considerations 249

Light and Photosynthesis in the Intact Leaf 250 The Architecture and Composition of a Leaf Maximize Light Absorption 251 Chloroplast Rearrangement and Leaf Movement Can Change the Amount of

Light Absorbed by the Leaf 252 Plant Growth and Development Often Reflect Competition for Sunlight 253 The Photosynthetic Response to Light in the Intact Leaf Reflects Basic Properties

of the Photosynthetic Apparatus 254 Leaves Must Dissipate Vast Quantities of Heat 254 Plants, Leaves, and Cells Adapt to Their Light Environment 255 Carbon Dioxide and Photosynthesis in Leaves 256 The Supply of CO_2 for Photosynthesis Depends on the Diffusion of CO_2 from the Atmosphere to the Chloroplast 256

There Is a Cost in Water for Every Mole of CO₂ Taken Up by the Leaf 259 Both Stomatal and Nonstomatal Factors Can Limit Photosynthesis 259 Photosynthetic Carbon Fixation in Guard Cells Could Serve as a Signal Between

the Stomata and the Mesophyll 260

CO₂ Concentrating Mechanisms Affect the Photosynthetic Response of the Intact Leaf 260

Temperature Responses of Photosynthesis 261 Summary 262

ESSAY \

Working With Gases 257 General Reading 263 Chapter References 263

CHAPTER 11 Respiration and Lipid Metabolism 265

Respiration 265

- In Glycolysis, Glucose Is Converted into Pyruvate and the Energy Released Is Stored in NADH and ATP 267
- In the Absence of O₂, Fermentation Allows the Regeneration of NAD⁺ Needed for Glycolysis 268
- Plants Can Also Use the Glycolytic Pathway in the Reverse Direction to Synthesize Glucose 268

Anaerobic Fermentation Liberates Only a Fraction of the Energy Available in Each Molecule of Sugar 269

Mitochondria Are Semiautonomous Organelles Surrounded by a Double Membrane 269

Pyruvate Is Oxidized in the Mitochondrion via the TCA Cycle 270

The TCA Cycle of Plant Cells Has Some Unique Features 272

The Electron Transport Chain of the Mitochondrion Catalyzes an Electron Flow from NADH to O_2 272

Some of the Electron Carriers of Plant Mitochondria Are Absent from Animal Mitochondria 275

ATP Synthesis in the Mitochondrion Is Coupled to Electron Transport 275

Aerobic Respiration Yields 32 Molecules of ATP per Molecule of Glucose 277 Plants Have a Cyanide-Resistant Respiration Pathway Not Found in Animals 278

Respiration Is Regulated by Energy Demand and the Concentration of Key Metabolites 278

The Pentose Phosphate Pathway Oxidizes Glucose to Ribulose 5-Phosphate and Reduces NADPH 279

Respiration is Tightly Coupled to Other Metabolic Pathways in the Cell 282 Whole Plant Respiration 282

Different Tissues and Organs Respire at Different Rates 282

Environmental Factors Can Alter Respiration Rates 282

Lipid Metabolism 284

Fats and Oils Are Triglycerides and Are Stored in Spherosomes 284

Triacylgycerol Biosynthesis Is Energetically Expensive and Takes Place in Several Cell Organelles 286

Phospholipid Biosynthesis Occurs in the ER and Mitochondrial Membranes 286

In Germinating Seeds, Lipids Are Converted into Carbohydrates 288 Summary 290

ESSAY Does Respiration Reduce Crop Yields? 283

General Reading 291

Chapter References 291

CHAPTER 12 Assimilation of Mineral Nutrients 292

Nitrogen Assimilation 292 Nitrogen Occurs in Several Forms That Are Interconverted in the Nitrogen Cycle 292 Biological Nitrogen Fixation Is Carried Out by Both Free-Living and Symbiotic Bacteria 293 The First Step in the Establishment of Symbiotic Nitrogen Is the Attachment of Rhizobium to the Root 296 Infection of Legume Roots by Rhizobium Is Facilitated by the Formation of an Infected Thread 298 The Biochemical Process of Nitrogen Fixation Is Carried Out by the Nitrogenase Enzyme Complex 300 The Nitrate Assimilation Pathway 302 Nitrate Is Taken Up by an Inducible Transport System 302 Nitrate Absorbed by Plants Is Reduced to Nitrite by Nitrate Reductase 302 Nitrate Reductase Is an Inducible Enzyme 303 Nitrite Is Reduced to Ammonium by Nitrite Reductase 303 The Anatomical Site of Nitrate Metabolism Differs According to Growth Conditions, Plant Age, and Plant Species 304 Ammonia Is Rapidly Incorporated into Organic Compounds 305 Nitrogen Is Incorporated into Other Amino Acids Through Transamination Reactions 305 The Major Export Forms of Nitrogen in Nitrogen-Fixing Plants Are Amides and Ureides 305 Sulfur Assimilation 307 Sulfate Must Be Reduced Prior to Assimilation into Carbon Compounds 307 Phosphate Assimilation 310 Cation Assimilation 310 Cation Complexes with Carbon Compounds Involve the Formation of Coordination or Electrostatic Bonds 310 Iron Assimilation Involves Redox Reactions and Complex Formation 311 Oxygen Assimilation 313 Summary 314 -ESSAY The Genes Involved in Symbiotic Nitrogen Fixation 297 - General Reading 315 Chapter References 315

CHAPTER 13 Surface Protection and Secondary Defense Compounds 318

Cutin, Suberin, and Waxes 318 Cutin, Suberin, and Waxes Are Made Up of Saturated Long-Chain Carbon Compounds 318 Cutin, Waxes, and Suberin Help Reduce Transpiration and Pathogen Invasion 320 Secondary Plant Products 320 The Principal Function of Secondary Plant Products Is to Defend Plants Against Herbivore and Pathogen Attack 320 Plant Defenses Evolved Because Herbivores and Pathogens Reduce Evolutionary Fitness 320 There Are Three Principal Groups of Secondary Products Based on Biosynthetic Criteria 321 Terpenes 322 Terpenes Are Formed by the Fusion of Five-Carbon Units 322

The Five-Carbon Building Blocks of Terpenes Are Synthesized by the Mevalonic Acid Pathway 323 Terpenes Serve as Antiherbivore Defense Compounds in Many Plants 324 Some Herbivores Can Circumvent the Toxic Effects of Terpenes and Other Secondary Plant Products 327 Phenolic Compounds 328 Most Plant Phenolics Are Synthesized from Phenylalanine, a Product of the Shikimic Acid Pathway 328 Simple Phenolics Take Part in Plant-Herbivore, Plant-Fungus, and Plant-Plant Interactions 330 Simple Phenolics That Escape into the Environment May Affect the Growth of Other Plants 331 Lignin Is a Complex Phenolic Macromolecule with Both Primary and Secondary Roles 331 The Flavonoids Form a Large Group of Phenolic Compounds Whose Structures Are Formed by the Action of Two Different Biosynthetic Pathways 333 Anthocyanins Are Colored Flavonoids Found in Flowers and Fruit That Help Attract Animals for Pollination and Seed Dispersal 334 Flavonoids Are Thought to Serve as Defenses and UV Protectants as Well as Attractants 335 Isoflavonoids Act as Antifungal and Antibacterial Defenses Called Phytoalexins, Which Are Synthesized Immediately Following Pathogen Infection 336 Tannins Are Polymeric Phenolic Compounds That Function as Feeding Deterrents to Herbivores 337 Nitrogen-Containing Compounds 338 Alkaloids Are Nitrogen-Containing Heterocyclic Compounds That Have Marked Physiological Effects on Animals 339 Cyanogenic Glycosides Release Hydrogen Cyanide When the Plant Tissue Containing Them Is Damaged by Herbivores 341 Glucosinolates or Mustard Oil Glycosides Also Release Volatile Toxins When the Plant Is Damaged 341 Certain Plants Contain Unusual Amino Acids That Are Not Constituents of Proteins but Function as Antiherbivore Defenses 342 Certain Plant Proteins Selectively Inhibit the Protein-Digesting Enzymes of Herbivores 342 Many Plant Secondary Products Can Be Catabolized Back to Primary Metabolic Intermediaries 343 The Distribution of Defensive Secondary Products Within Plants 343 Plants Are Not Usually Poisoned by Their Own Toxic Secondary Metabolites 343 Summary 343 Salicylic Acid and Thermogenesis in Arum Lilies 332 ESSAY A Bee's-Eye View of a Golden-Eye's "Bull's Eye" 335 Chapter References 344 General Reading 344

CHAPTER 14 Stress Physiology 346

ESSAY

Water Deficit and Drought Resistance 347 Drought Resistance Strategies Vary With Climatic or Soil Conditions 347 Decreased Leaf Area Is an Early Response to Water Deficit 348 Water Deficit Stimulates Leaf Abscission 348 Water Deficit Enhances Root Extension into Deeper, Moist Soil 349 Stomata Close During Water Deficit in Response to Abscisic Acid 350 Water Deficit Limits Photosynthesis Within the Chloroplast 352 Osmotic Adjustment of Cells Helps Maintain Plant Water Balance 353

Water Deficit Alters Energy Dissipation from Leaves 354 Water Deficit Increases Resistances to Liquid-Phase Water Flow 355 Water Deficit Increases Wax Deposition on the Leaf Surface 356 Water Deficits May Induce Crassulacean Acid Metabolism 356 Chilling and Freezing 356 Membrane Properties Change upon Chilling Injury 356 Freezing Kills Cells Because of the Formation of Large Intracellular Ice Crystals 358 Acclimation to Freezing Involves ABA and Changes in Gene Expression 358 Some Woody Plants Can Acclimate to Very Low Temperatures 358 Deep Supercooling and Dehydration Are Involved in Resistance to Intracellular Freezing 358 Some Bacteria Living on Leaf Surfaces Increase Frost Damage 360 Heat Stress and Heat Shock 360 At High Temperatures, Photosynthesis Is Inhibited Before Respiration 361 Plants Adapted to Cool Temperatures Acclimate Poorly to High Temperatures 361 High Temperature Impairs the Thermal Stability of Membranes and of Proteins 361 Several Adaptations Protect Leaves Against Excessive Heating 362 Abrupt Increases in Temperature Induce Synthesis of Heat Shock Proteins 362 Salinity 362 Salt Accumulation in Soils Impairs Plant Function and Soil Structure 363 Salinity Depresses Growth and Photosynthesis in Sensitive Species 363 Salt Injury Involves Both Osmotic Effects and Specific Ion Effects 363 Plants Use Different Strategies to Avoid Salt Injury 364 Salt Stress Induces Synthesis of New Proteins 364 Oxygen Deficiency 365 Roots Are Injured in Anaerobic Soil Water 365 The Failure of O₂-Deficient Roots to Function Injures Shoots 365 Submerged Organs Can Acquire O₂ Through Specialized Structures 366 Some Plant Tissues Tolerate Anaerobic Conditions 367 Acclimation to O₂ Deficit Involves Production of Anaerobic Stress Proteins 367 Air Pollution 367 Polluting Gases Inhibit Stomatal Movements, Photosynthesis, and Growth 368 Polluting Gases, Dissolved in Rainwater, Fall as "Acid Rain" 368 Summary 368 ESSAY Gene Action During Water Deficit 351 ESSAY Ice Formation in Higher Plant Cells 359 General Reading 369 Chapter References 369

UNIT III



GROWTH AND DEVELOPMENT 371

CHAPTER 15 The Cellular Basis of Growth and Morphogenesis 373

Anatomical and Ultrastructural Aspects of Growth 373 Plant Growth Is Defined as a Permanent Increase in Size 373 Specialized Growth Zones Contribute to Primary and Secondary Growth 374

	Primary Roots Can be Divided into Four Zones 3/6 Primary Shoot Growth Gives Rise to Phytomers: Nodes and Internodes 377
	Plant Cell Expand by Two Mechanisms: Tip Growth and Diffuse Growth 377
	Polarity Is a Property of Organs and Cells 378
	Polarity in Tip-Growing Cells 378
	A Transcellular Current Is the Earliest Manifestation of Polarity 378
	Actin Microfilaments and Cell Wall Deposition Stabilize the Polarity of the Axis 378
	The Position of the Nucleus Can Also Influence Polarity 380
	Polarity in Diffuse-Growing Cells 381
	The Direction of Cell Expansion in Diffuse-Growing Cells Is Determined by the
	Orientation of Cellulose Microfibrils 381
	Microtubule Orientation Mirrors the Orientation of Newly Deposited Cellulose Microfibrils 382
	Control of the Plane of Cell Division 384
	During Cell Division, Microtubules Form the Preprophase Band, the Mitotic
	Spindle, and the Phragmoplast 385
	The Plane of Cell Division Is Determined Before Mitosis 385
	Differentiation of Selected Cell Types 386
	In Iracheary Elements, Microtubules Determine the Pattern of Secondary Wall Thickenings 386
	The Differentiation of Stomatal Complexes Depends on the Precise Placement of
	Cross-Walls During Cytokinesis 387
	Morphogenesis in Roots and Shoots 389
	Cell-Cell Communication Occurs Symplastically via Plasmodesmata or
	Apoplastically I nrough the Cell Wall 390 Roots of the Water Form Acalla House Boon Used for Historical Analysis of Cell
	Lineages 390
	Microtubule and Microfibril Rearrangements on the Outer Epidermal Wall
	Precede the Formation of a New Axis 392
	The Cell Cycle May Influence the Ability of a Cell to Differentiate 394
	Summary 396
ESSAY	Clonal Analysis of Shoot Development 391
_	General Reading 396
	Chapter References 396
CHAPTER 16	Auxins: Growth and Tropisms 398
	Chemistry, Metabolism, and Transport 399
	The Principal Auxin in Higher Plants Is Indole-3-Acetic Acid 399
	Three Techniques Are Used for Detection and Analysis of Auxins 399
	Plants Contain Bound Auxins 403
	Auxin Levels Are Controlled by the Rates of Synthesis and Degradation 404
	Auxin is Iransported Both Passively and Actively 405
	Polar Auxin Transport Involves Basally Located Carrier Proteins 406
	Auving Induce Cell Florention in Stems and Colooptiles 409
	Auxin Increases the Extensibility of the Cell Wall 408

Does Auxin Regulate Growth in Roots and Leaves? 410

Tropisms Are Growth Responses to Directional Stimuli 411

Action Spectra for Phototropism Have Peaks in the Visible and the Near-Ultraviolet 411

Phototropism May Be Mediated by the Lateral Redistribution of Auxin 412 Gravitropism in Shoots Involves Auxin Redistribution 413

Statoliths in the Cap Cells Direct the Transport of an Inhibitor to the Lower Side of a Horizontal Root 414

Auxin from the Apical Bud Inhibits the Growth of Lateral Buds 415 Auxin Promotes the Formation of Lateral Roots 416 Auxin Delays the Onset of Leaf Abscission 416 Auxin Regulates in Fruit Development 416 Synthetic Auxins Have a Variety of Commercial Uses 417 The Mechanism of Auxin Action 417 The Lag Time for Auxin-Induced Growth is 15–20 Minutes 417 Intracellular Second Messengers May Mediate Plant-Hormone Action 417 Several Potential Auxin Receptors Have Been Identified 418 Auxin Action May Involve Calcium Fluxes 420 Auxin Regulates the Expression of Specific Genes 420 Summary 423 ESSAY The Biophysics of Plant Cell Expansion 409 General Reading 424 Chapter References 424 CHAPTER 17 Gibberellins 426 Discovery 426 Biosynthesis 428 Gibberellins Are Made Up of Isoprene Units 429 Oxidations and Hydroxylations of GA₁₂, Yield All the Other Gibberellins 429 Most Gibberellins Are Precursors of Bioactive Gibberellins 431 Gibberellins May Also Be Conjugated to Sugars 433 Detection and Assay 433 Bioassays Detect and Measure Gibberellin-Like Compounds 433 Gas Chromatography-Mass Spectrometry Provides Definitive Analysis of Gibberellins 435 The Physiological Effects of Gibberellins 437 Applied Gibberellins Produce a Range of Effects in Plants 438 Endogenous GA₁ Regulates Stem Elongation 439 Some Plants Grow Unusually Tall in the Absence of Gibberellins 441 Photoperiod May Regulate Gibberellin Metabolism 441 The Mechanism of Gibberellin Action 443 - Gibberellins Increase Cell Wall Extensibility in Gibberellin-Responsive Stems 444 Gibberellins From the Embryo Stimulate α -Amylase Production in Cereal Seeds 444 Gibberellic Acid Enhances the Transcription of α -Amylase mRNA 446 DNA-Binding Proteins Regulate the Transcription of α -Amylase 446 The Gibberellin Receptor May Be Located on the Plasma Membrane of Aleurone Cells 448 **Commercial Applications of Gibberellins** 448 Summary 449 ESSAY The Mass Spectrometer 434 General Reading 450 Chapter References 450 452

CHAPTER 18 Cytokinins

Cell Division in Plant Development 452 Differentiated Plant Cells Can Resume Division 452 Diffusible Factors May Control Cell Division 453 Plant Tissues and Organs Can Be Cultured 453 The Discovery and Identification of Cytokinins 454 The Discovery of Kinetin, a Synthetic Cytokinin 454

Zeatin Is the Naturally Occurring Cytokinin of Most Plants 454 Some Synthetic Compounds Can Mimic or Antagonize Cytokinin Action 456 A Variety of Methods Are Used to Assay for Cytokinins 456 Naturally Occurring Cytokinins Are Both Free and Bound 457 Some Bacteria Also Secrete Free Cytokinins 458 Biosynthesis, Metabolism, and Transport of Cytokinins 458 Cytokinin Synthase Catalyzes the First Step in Cytokinin Biosynthesis 458 Modification of the Polymerized Base Produces the tRNA Cytokinins 458 Cytokinins Synthesized in the Root Are Transported to the Shoot in the Transpiration Stream 459 Cultured Cells Can Acquire the Ability to Synthesize Cytokinins 460 Cytokinin Synthesis by Crown Gall Tissues Results from Genetic Transformation of Plant Cells 460 Cytokinin Nucleotides Are the Predominant Form in the Xylem 463 The Free Base Is Probably the Active Form of the Hormone 463 The Biological Role of Cytokinins 463 The Cell Cycle in Plants Has Two Control Points 463 Hormones May Regulate the Plant Cell Cycle 464 The Auxin/Cytokinin Ratio Regulates Morphogenesis in Cultured Tissues 464 Cytokinins Delay Senescence and Stimulate Nutrient Mobilization 465 Cytokinins Promote the Maturation of Chloroplasts 465 Cytokinins Can Stimulate Cell Enlargement 466 The Mechanism of Cytokinin Action Plant Cells Contain Cytokinin-Binding Proteins 467 Cytokinins Regulate Protein Synthesis 467 Cytokinins Affect a Posttranscriptional Step in Lemna 468 The Cytokinins in tRNA May Regulate Protein Synthesis 469 Cytokinins Regulate Calcium Concentration in the Cytosol 469 Summary 470 ESSAY The Ti Plasmid and Plant Genetic Engineering 462 General Reading 471 Chapter References 471

CHAPTER 19 Ethylene and Abscisic Acid 473

Transport 484

Ethylene 473

The Properties of Ethylene are Deceptively Simple 474 Bacteria, Fungi, and Plant Organs Produce Ethylene 474 Biosynthesis and Catabolism Determine the Physiological Activity of Ethylene 474 Environmental Stresses and Auxins Promote Ethylene Biosynthesis 476 Both Ethylene Production and Ethylene Action Can Be Blocked by Specific Inhibitors 476 Ethylene Can Be Measured in Bioassays or by Gas Chromatography 477 Ethylene Has Numerous Effects on Different Plant Species and Organs 478 The Mechanism of Ethylene Is Not Well Understood 481 Ethylene Has Important Commercial Uses 481 Abscisic Acid 482 ABA Is Widely Distributed in Nature 482 The Chemical Structure of ABA Determines Its Physiological Activity 483 ABA Is Assayed by Biological, Physicochemical, and Immunological Methods 484 The Amount of ABA in a Tissue Depends on Its Biosynthesis, Metabolism, and ABA Causes Many Physiological Responses in Higher Plants 485 ABA Regulates Protein Synthesis 487 Summary 487 General Reading 488 Chapter References 488

CHAPTER 20 Phytochrome and Photomorphogenesis 490

The Photochemical and Biochemical Properties of Phytochrome 490 The Two Forms of Phytochrome Are Interconvertable 491 There Are Short-Lived Intermediates Between Pr and Pfr 492 In Most Cases Pfr Is the Physiologically Active Form 492 The Amount of Pfr Can Be Regulated by Synthesis, Breakdown, and Dark Reversion 493 Two Types of Phytochrome Have Been Identified 493 Two 124-kDa Monomers Make Up the Phytochrome Dimer 494 Phytochrome Undergoes Subtle Conformational Changes 494 495 Phytochrome Localization in Tissues and Cells Phytochrome Can Be Detected in Tissues Spectrophotometrically 495 Immunocytochemical Methods Have Revealed Where Phytochrome Is Concentrated in Tissues and Cells 495 Photoreversible Responses Have Been Measured in Isolated Organelles 496 Phytochrome-Induced Whole Plant Responses 497 Phytochrome Responses Vary in Lag Time and Escape Time 497 Phytochrome Effects on Plants Can Be Classified According to the Quantity of Light Required 497 Phytochrome Enables Plants to Adapt to Changes in Light Conditions 498 Phytochrome Regulates Certain Daily Rhythms 500 Cellular and Molecular Mode of Action 500 Phytochrome Can Associate with Membranes 501 Calcium and Calmodulin May Mediate Some Pfr Responses 505 Phytochrome Regulates Gene Transcription 508 The Promoter Region of the *rbcS* Gene Is Light Regulated - 509 Phytochrome Regulates the Expression of Its Own Gene 510 Summary 511 Mougeotia: A Chloroplast with a Twist 502 General Reading 511 Chapter References 512

ESSAY

CHAPTER 21 The Control of Flowering 513

Effects of Plant Age 514
Apical Changes Are Important in the Transition from Juvenility to Maturity 515
The Apex Receives Both Nutrients and Hormones from the Plant 515
Photoperiodism 516
Plants Can Show Daily Rhythms in the Absence of External Changes 516
Daylength Is a Major Determinant of Flowering Time 518
Plants Track Daylength by Measuring the Length of the Night 520
An Endogenous Oscillator Is Involved in Photoperiodic Timekeeping 521
Phytochrome Is Involved in Photoperiodism 522
Far-Red Light Modifies Flowering in Some LDPs 523
Vernalization 524
Photoperiodism and Vernalization May Interact 525

Protein Synthesis Appears to Be Required for Vernalization 525

-

-

The Transition to Flowering526Photoperiodic Induction of a Single Leaf Can Cause Flowering526Identification of the Hypothetical Florigen Remains Elusive526Gibberellins Can Induce Flowering in Some Plants528The Floral Stimulus May Have Several Components528Summary529ESSAYGene Expression During Flower Development527General Reading530Chapter References530AUTHOR INDEX533SUBJECT INDEX539